

# R2ucare: An R package to perform goodness-of-fit tests for capture-recapture models

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## Summary:

1. Assessing the quality of fit of a statistical model to data is a necessary step for conducting safe inference.
2. We introduce R2ucare, an R package to perform goodness-of-fit tests for open single- and multi-state capture-recapture models. R2ucare also has various functions to manipulate capture-recapture data.
3. We remind the basics and provide guidelines to navigate towards testing the fit of capture-recapture models. We demonstrate the functionality of R2ucare through its application to real data.

**Keywords:** Arnason-Schwarz, capture-mark-recapture, Cormack-Jolly-Seber, model validation, R2ucare

## Introduction

Capture-recapture (CR) models have become a central tool in population ecology for estimating demographic parameters under imperfect detection of individuals (Lebreton et al. 1992; 2009). These methods rely on the longitudinal monitoring of individuals that are marked (or identifiable) and then captured or sighted alive over time.

Single-state CR models, and the Cormack-Jolly-Seber (CJS) model in particular (Lebreton et al. 1992), have been used to assess the effect of climate change (e.g. Guéry et al. 2017) or study senescence (e.g. Péron et al. 2016). The extension of single-state models to situations where individuals are detected in several geographical sites or equivalently states (e.g. breeding/non-breeding or sane/ill) are called multi-state CR models (Lebreton et al. 2009). Multistate CR models, and the Arnason-Schwarz model in particular (Lebreton et al. 2009), are appealing for addressing various biological questions such as metapopulation dynamics (e.g. Spindel et al. 2016) or life-history trade-offs (e.g. Supp et al. 2015).

A necessary step for correct inference about demographic parameters is to assess the fit of single- and multi-state models to CR data, regardless of whether a Bayesian or a frequentist framework is adopted.

Two family of methods exist to perform goodness-of-fit (GOF) tests for CR models. First, an omnibus test of the null hypothesis that a given model fits the data adequately can be conducted using resampling methods and the deviance as a metric (White 2002). However when the null hypothesis is rejected, this omnibus approach does not inform about an alternative model that could be fitted. Second, specialized tests have been built to address biologically meaningful causes of departure from the null hypothesis. A global test for single- and multi-state CR models is decomposed into several interpretable components based on contingency tables, for example the presence of transients (Pradel et al., 1997; Pradel et al. 2003) or that for trap-dependence (Pradel, 1993; Pradel et al. 2003). These GOF tests are implemented in the Windows application U-CARE (Choquet et al. 2009).

Here, we introduce the R (R Development Core Team 2014) package R2ucare to perform GOF tests for single- and multi-state CR models. R2ucare also includes various functions to help manipulate CR data. As a package in the CRAN database, R2ucare provides full advantage of R's many features (e.g. simulations, model fitting), while being multi-platform. We go through the theory first, then illustrate the use of R2ucare with an example on wolf in France for single-state models and geese in the U.S. for multi-state models.

## Theory

Once a model has been specified, GOF testing is the procedure that controls model assumptions. GOF testing and model fitting are two complementary procedures that share and compete for the information contained in the data. More liberal models require more information to be fitted (there are more parameters to estimate) but also fewer assumptions need to be verified. For instance, the time-dependent CJS model is merely content with the numbers of individuals captured at each occasion and the numbers never seen again from those released at each occasion when it comes to estimating its parameters. These summary statistics leave much of the details of the capture histories available to test its assumptions.

There are several ways in which this remaining information may be exploited to test the assumptions. The implementation retained in R2ucare builds on the optimal approach originally devised by Pollock et al. (1985) and later modified by Pradel (1993). It is based on contingency tables and aims at testing with chi-squared tests (and Fisher's exact tests when needed) for transients and trap-dependence. These aspects are examined specifically in two independent component tests called respectively Test 3.SR and Test 2.CT. The component tests directed at transients and trap-dependence actually address features of the data that are consequences of respectively the presence of transients and trap-dependence, so that these features may also be caused by other, completely different phenomena. They do verify respectively that:

- Newly encountered individuals have the same chance to be later reobserved as recaptured (previously encountered) individuals; this is the null hypothesis of Test 3.SR.
- Missed individuals have the same chance to be recaptured at the next occasion as currently captured individuals; this is the null hypothesis of Test 2.CT.

Although these components are often called 'test of transience' and 'test of trap-dependence', when it comes to interpretation, one should keep in mind that transience and trap-dependence are just two specific reasons why the tests respectively called 3.SR and 2.CT might be significant.

Interestingly, these two components provide formal tests for comparing the CJS model with more general models, namely a model with an interaction between age (2 classes) and time in the survival probability for Test 3.SR (Pradel et al. 1997) and a model allowing for a different recapture probability of individuals just released for Test 2.CT (Pradel 1993).

Beyond these two oriented components, the remaining information is distributed and structured into two additional components: Test 3.Sm and Test 2.CL. Those examine long-term features of the data:

- Among those individuals seen again, when they were seen does not differ among previously and newly marked individuals; this is the null hypothesis of Test 3.Sm.
- There is no difference in the timing of reencounters between the individuals encountered and not encountered at occasion  $i$ , conditional on presence at both occasions  $i$  and  $i + 2$ ; this is the null hypothesis of Test 2.CL?

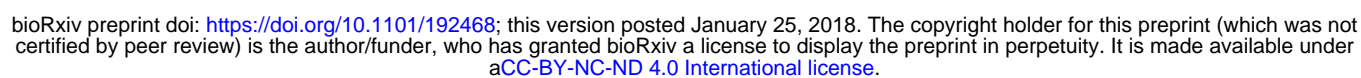
Data are generally sparse for these components and scattered over many occasions. Despite the implementation of some automatic pooling (see Choquet et al. 2005 for more details about the pooling rules), they are rarely significant alone.

Although many situations can lead to similar test results, we propose here a decision tree (Figure 1) that should lead to reasonable solutions in most cases.

The theory for the GOF test of the multistate Arnason-Schwarz model was developed along similar lines as for the CJS model (Pradel et al. 2003). This test has yet more components and some components have a more complex structure (hence our non attempt to build a decision tree as for the CJS model), but for all that concerns us, the reasoning remains very similar. The test implemented in R2ucare is actually a test of the Jolly-Move model, a slightly more general model than the Arnason-Schwarz model in that it allows detection parameters to depend on the previous state occupied. This is biologically irrelevant in most common situations (Pradel et al. 2003), so that we may reason as if we were examining the Arnason-Schwarz model. Components here have been designed to detect transients, trap-dependence, and the memory of past states. This last point means that the component examines whether transitions to a new state depend on previous states beyond the current one. The corresponding components are respectively Test 3.GSR, Test M.ITEC, and Test WBWA. Like for the CJS case, they actually examine features of the data, namely that:

- Newly encountered individuals have the same chance to be later reobserved as recaptured (i.e. previously encountered) individuals; this is the null hypothesis of Test 3.GSR which is the exact equivalent of 3.SR.
- Individuals currently in the same state, whether captured or missed, have the same chance to be recaptured in each state at the next occasion; this is the null hypothesis of Test M.ITEC.
- Individuals currently captured in the same state have the same chance to be next reobserved in the different states independently of their observed state at the most recent capture; this is the null hypothesis of Test WBWA.

These interpretable components are complemented by two composite components with no clearly identified interpretation, Test 3.GSm and Test M.LTEC. We do not attempt to give a de-



scription of these; let it suffice to say that Test 3.SM is concerned with comparing newly and previously encountered, while Test M.LTEC contrasts missed and encountered individuals. Fortunately, these components play a secondary role as they are usually not significant alone.

For more details about the theory of GOF testing for CR models, we strongly encourage users to read Pradel et al. (2005) and Cooch and White (2006).

## The R2ucare package

The R2ucare package contains R functions to perform GOF tests for CR models as well as various functions to manipulate CR data (see Table 1 and the vignette of the package named `vignette_R2ucare`). It ensures reproducibility which was not possible with the U-CARE (Choquet et al. 2009) Windows standalone application. Besides, it can be used in combination with other R packages for fitting CR data like RMark (Laake 2013) or marked (Laake et al. 2013) or to carry out simulations to assess statistical power (e.g. Bromaghin et al. 2013; Fletcher et al. 2012).

Table 1: The main functions of R2ucare and their description. See main text for more details.

Function	Description
<code>marray</code>	build a m-array for single-site/state capture-recapture data
<code>multimarray</code>	build a m-array for multi-site/state capture-recapture data
<code>group_data</code>	pool together individuals with the same encounter capture-recapture history
<code>ungroup_data</code>	split encounter capture-recapture histories into individual ones
<code>read_inp</code>	read MARK formatted files
<code>read_headed</code>	read E-SURGE formatted files
<code>test3sr</code>	implement Test 3.SR for single-site/state models (presence of transients)
<code>test3sm</code>	implement Test 3.SM for single-site/state models
<code>test2ct</code>	implement Test 2.CT for single-site/state models (presence of trap-dependence)
<code>test2cl</code>	implement Test 2.CL for single-site/state models

Function	Description
test3Gsr	implement Test 3.GSR for multi-site/state models (presence of transients)
test3Gsm	implement Test 3.GSm for multi-site/state models
test3Gwbwa	implement Test WBWA for multi-site/state models (presence of memory)
testMitec	implement Test M.ITEC for multi-site/state models (presence of trap-dependence)
testMltec	implement Test M.LTEC for multi-site/state models

## Goodness-of-fit tests for single-site/state models

We illustrate the use of R2ucare to assess the GOF of the CJS model to a dataset on wolves (*Canis lupus*) in France (e.g., Fletcher et al. 2012). Briefly, the data consist of capture histories for 160 individuals, partitioned into 35 3-month intervals (from spring 1995 to autumn 2003).

We first load the R2ucare package:

```
library(R2ucare)
```

Then we read in the wolf data that is provided with the package. To do so, R2ucare contains two functions that accomodate the most frequent CR formats: `read_inp` deals with the MARK format (Cooch and White 2006) while `read_headed` deals with the E-SURGE format (Choquet et al. 2009). The wolf dataset has the MARK format, therefore:

```
wolf = system.file("extdata", "wolf.inp", package = "R2ucare")
wolf = read_inp(wolf)
```

We then get the matrix and number of CR encounter histories:

```
ch = wolf$encounter_histories
n = wolf$sample_size
```

Following the procedure described in Figure 1, we first assess the overall fit of the CJS model by using the function `overall_CJS`:

```
overall_CJS(ch,n)
```

```
139 ##                                chi2 degree_of_freedom p_value
140 ## Gof test for CJS model: 180.73                115          0
```

141 Clearly, the CJS model does not fit the data well ( $\chi^2_{115} = 180.73$ ,  $P < 0.01$ ). We then test for an  
142 effect of trap-dependence:

```
test2ct(ch,n,verbose = FALSE)
```

```
143 ## $test2ct
144 ##      stat      df      p_val sign_test
145 ##    64.451    31.000    0.000    -5.641
```

146 Test 2.CT is significant ( $\chi^2_{31} = 64.45$ ,  $P < 0.01$ ). We also provide the signed square root  
147 (sign\_test) of the Pearson chi-square statistic as a directional test of the null hypothesis (Pradel et  
148 al. 2005), which is negative when there is an excess of individuals encountered at a given occasion  
149 among the individuals encountered at the previous occasion.

150 Note that, by default, the GOF functions in R2ucare returns all the contingency tables that  
151 compose the test under scrutiny, which might not be of immediate use and rather cumbersome  
152 on screen, hence the use of verbose=FALSE in the call to the test2ct function above. Now we ask  
153 whether there is a transient effect:

```
test3sr(ch,n,verbose = FALSE)
```

```
154 ## $test3sr
155 ##      stat      df      p_val sign_test
156 ##    65.414    29.000    0.000     5.037
```

157 Test 3.SR is also significant ( $\chi^2_{29} = 65.41$ ,  $P < 0.01$ ). We also provide the signed square root  
158 (sign\_test) of the Pearson chi-square statistic (Pradel et al. 2005), which is positive when there is  
159 an excess of never seen again among the newly marked.

160 Navigating through the decision tree in Figure 1 suggests we should perform the two remain-  
161 ing tests:



```
test3sm(ch,n,verbose = FALSE)
```

```
162 ## $test3sm
163 ##      stat      df  p_val
164 ## 22.977 25.000  0.579
```

```
test2cl(ch,n,verbose = FALSE)
```

```
165 ## $test2cl
166 ##      stat      df  p_val
167 ## 27.888 30.000  0.576
```

168 Neither Test 3.Sm ( $\chi^2_{25} = 22.98, P = 0.58$ ) nor Test 2.CL ( $\chi^2_{30} = 27.89, P = 0.58$ ) is significant,  
 169 therefore we recommend fitting a CJS model incorporating both a transience effect and a trap-  
 170 dependence effect and start the analysis from there. In passing, it is possible to calculate a GOF  
 171 test for this new model by removing the two components Test 3.SR and Test 2.CT to the overall  
 172 GOF test (Pradel et al. 2005):

```
# subtract the components 3SR and 2CT to the CJS test statistic
stat_new = overall_CJS(ch,n)$chi2 - (test3sr(ch, n)$test3sr[[1]]
                                     + test2ct(ch, n)$test2ct[[1]])

# calculate degree of freedom associated with the new test statistic
df_new = overall_CJS(ch,n)$degree_of_freedom -
          (test3sr(ch, n)$test3sr[[2]] + test2ct(ch, n)$test2ct[[2]])

# compute p-value
1 - pchisq(stat_new, df_new)
```

```
173 ## [1] 0.6332861
```

174 This new model incorporating transient and trap-dependence effects fits the wolf data well  
 175 ( $\chi^2_{55} = 50.87, P = 0.63$ ).

176 To date, no GOF test exists for models with individual covariates (unless we discretize them  
 177 and use groups), individual time-varying covariates (unless we treat them as states) or temporal

covariates; therefore, these covariates should be removed from the dataset before using R2ucare. For groups, we recommend treating the groups separately (see e.g. the example in the help file for overall\_CJS).

## Goodness-of-fit tests for the Arnason-Schwarz model

We now wish to assess the GOF of the Arnason-Schwarz model to a dataset on Canada Geese (*Branta canadensis*) (Pradel et al. 2005). Briefly, the data consist of capture histories for 28,849 individuals marked and re-observed at wintering locations in the US between 1984 and 1986.

We first read in the geese data that are provided with the package:

```
geese = system.file("extdata", "geese.inp", package = "R2ucare")
geese = read_inp(geese)
```

We then get the matrix and number of CR encounter histories:

```
ch = geese$encounter_histories
n = geese$sample_size
```

Then we assess the quality of fit of the Arnason-Schwarz model to the geese CR data with the overall\_JMV function. Beware that it takes a minute or so to run the test because an iterative optimization procedure is involved to perform Test M.ITEC and Test M.LTEC (Pradel et al. 2003) that is repeated several times to try and avoid local minima.

```
overall_JMV(ch,n)
```

```
##                                chi2 degree_of_freedom p_value
## Gof test for JMV model: 982.599                197          0
```

The null hypothesis that the Arnason-Schwarz provides an adequate fit to the data is clearly rejected ( $\chi^2_{197} = 982.59$ ,  $P < 0.01$ ). In a second step, we further explore each component of the overall test:

```
test3Gsr(ch,n,verbose=FALSE) # transience
```

```
196 ## $test3Gsr
197 ##      stat      df    p_val
198 ## 117.753  12.000    0.000
```

```
test3Gsm(ch,n,verbose=FALSE)
```

```
199 ## $test3Gsm
200 ##      stat      df    p_val
201 ## 302.769 119.000    0.000
```

```
test3Gwbwa(ch,n,verbose=FALSE) # memory
```

```
202 ## $test3Gwbwa
203 ##      stat      df    p_val
204 ## 472.855  20.000    0.000
```

```
testMitec(ch,n,verbose=FALSE) # short-term trap-dependence
```

```
205 ## $testMitec
206 ##      stat      df    p_val
207 ## 68.227  27.000    0.000
```

```
testMltec(ch,n,verbose=FALSE) # long-term trap-dependence
```

```
208 ## $testMltec
209 ##      stat      df    p_val
210 ## 20.987  19.000    0.338
```

211 It appears that all components are significant but the test for a long-term trap-dependence  
 212 effect. By setting the verbose argument to TRUE (by default argument), one could closely examine  
 213 the individual contingency tables and better understand the reasons for the departure to the null  
 214 hypotheses. For example, let us redo the test for transience Test 3.GSR:

```
test3Gsr(ch,n,verbose=TRUE)
```

```
215 ## $test3Gsr
216 ##      stat      df    p_val
217 ## 117.753  12.000    0.000
218 ##
219 ## $details
220 ##      occasion site      stat df      p_val  test_perf
221 ## 1           2      1 3.894777e-03  1 9.502378e-01 Chi-square
222 ## 2           2      2 2.715575e-04  1 9.868523e-01 Chi-square
223 ## 3           2      3 8.129814e+00  1 4.354322e-03 Chi-square
224 ## 4           3      1 1.139441e+01  1 7.366526e-04 Chi-square
225 ## 5           3      2 2.707742e+00  1 9.986223e-02 Chi-square
226 ## 6           3      3 3.345916e+01  1 7.277633e-09 Chi-square
227 ## 7           4      1 1.060848e+01  1 1.125702e-03 Chi-square
228 ## 8           4      2 3.533332e-01  1 5.522323e-01 Chi-square
229 ## 9           4      3 1.016778e+01  1 1.429165e-03 Chi-square
230 ## 10          5      1 1.101349e+01  1 9.045141e-04 Chi-square
231 ## 11          5      2 1.292013e-01  1 7.192616e-01 Chi-square
232 ## 12          5      3 2.978513e+01  1 4.826802e-08 Chi-square
```

233 By inspecting the data.frame containing the details of the test, we see that there is no transients  
234 in site 2.

## 235 Future directions

236 R2ucare allows evaluating the quality of fit of standard capture-recapture models for open pop-  
237 ulations. Future developments will focus on implementing goodness-of-fit tests for models com-  
238 bining different sources of data (McCrea et al. 2014) and residual-based diagnostics (Choquet et  
239 al. 2013, Warton et al. 2017).

## Availability

The current stable version of the package requires R 3.4.3 and is distributed under the GPL license.

It can be installed from CRAN and loaded into a R session as follows:

```
install.packages("R2ucare",dependencies=TRUE)
library("R2ucare")
```

The repository on GitHub <https://github.com/oliviergimenez/R2ucare> hosts the development version of the package, it can be installed as follows:

```
if(!require(devtools)) install.packages("devtools")
library("devtools")
install_github("oliviergimenez/R2ucare")
```

We also maintain a forum at [https://groups.google.com/forum/#!forum/esurge\\_ucare](https://groups.google.com/forum/#!forum/esurge_ucare) to which questions can be asked.

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Replication files (paper and code) are available on the first author's Github account (<https://github.com/oliviergimenez>).

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## Authors' contributions

OG, JDL and RP conceived the ideas and designed methodology; OG, JDL, RC and RP wrote the code; OG and RP led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## References

Bromaghin, J. F., T. L. McDonald, and S. C. Amstrup (2013) Plausible combinations: An improved method to evaluate the covariate structure of Cormack-Jolly-Seber mark-recapture models. *Open Journal of Ecology* 3: 11-22.

259 Choquet, R., Reboulet, A.-M., Lebreton, J.-D., Gimenez, O., and R. Pradel. (2005). U-CARE 2.2 user's  
260 manual. CEFE, UMR 5175, Montpellier.

261 Choquet, R., Lebreton, J.-D., Gimenez, O., Reboulet, A.-M., and R. Pradel. (2009). U-CARE: Utilities for  
262 performing goodness of fit tests and manipulating CAPture-REcapture data. *Ecography* **32**: 1071-1074.

263 Choquet, R., Rouan, L., Pradel, R. (2009). Program E-SURGE: A software application for fitting multievent  
264 models. Modeling Demographic Processes in Marked Populations. D. L. Thomson, E. G. Cooch and M.  
265 J. Conroy. Berlin, Germany, Springer. **3**: 845-865.

266 Choquet, R., Carrie, C., Chambert, T. & Boulinier, T. (2013). Estimating transitions between states using  
267 measurements with imperfect detection: application to serological data. *Ecology* **94**: 2160-2165.

268 Cubaynes, S., C. Lavergne, E. Marboutin, and O. Gimenez (2012). Assessing individual heterogeneity us-  
269 ing model selection criteria: How many mixture components in capture-recapture models? *Methods in*  
270 *Ecology and Evolution* **3**: 564-573.

271 Fletcher, D., Lebreton, J.-D., Marescot, L., Schaub, M., Gimenez, O., Slooten, E. and S. Dawson (2012). Bias  
272 in estimation of adult survival and asymptotic population growth rate caused by undetected capture  
273 heterogeneity. *Methods in Ecology and Evolution* **3**: 206-216.

274 Gimenez O., Choquet R. and J.-D. Lebreton (2003). Parameter redundancy in multistate capture-recapture  
275 models. *Biometrical Journal* **45**: 704-722.

276 Gimenez, O., Cam, E., and J.-M. Gaillard (2017). Individual heterogeneity and capture-recapture models:  
277 what, why and how? *Oikos*. In press. doi: 10.1111/oik.04532.

278 Guéry, L., Descamps, S., Pradel, R., Hanssen, S. A., Erikstad, K. E., Gabrielsen, G. W., Gilchrist, H. G. and  
279 Bêty, J. (2017). Hidden survival heterogeneity of three Common eider populations in response to climate  
280 fluctuations. *Journal of Animal Ecology* **86**: 683–693.

281 Jeyam, A., R. S. McCrea, T. Bregnballe, M. Frederiksen, and R. Pradel (2017). A test of positive association  
282 for detecting heterogeneity in capture for capture-recapture data. Submitted to *Journal of Agricultural,*  
283 *Biological, and Environmental Statistics*.

284 Laake, J. L. (2013). RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC  
285 Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way  
286 NE, Seattle WA 98115.

287 Laake, J. L., Johnson, D. S. and Conn, P. (2013). marked: An R package for maximum-likelihood and MCMC

analysis of capture-recapture data. *Methods in Ecology and Evolution* **4**: 885-890.

Lebreton, J.-D. et al. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* **62**: 67-118.

McCrea, R. S., B. J. T. Morgan, R. Pradel (2014). Diagnostic Goodness-of-Fit Tests for Joint Recapture and Recovery Models. *Journal of Agricultural, Biological, and Environmental Statistics* **19**: 338-356.

Péron, G., Crochet, P.A.C., Choquet, R., Pradel, R., Lebreton, J.-D. and O. Gimenez. (2010). Capture-recapture models with heterogeneity to study survival senescence in the wild. *Oikos* **119**: 524-532.

Péron, G., J.-M. Gaillard, C. Barbraud, C. Bonenfant, A. Charmantier, R. Choquet, T. Coulson, V. Grosbois, A. Loison, G. Marzolin, N. Owen-Smith, D. Pardo, F. Plard, R. Pradel, C. Toïgo, O. Gimenez (2016). Evidence of reduced individual heterogeneity in adult survival of long-lived species. *Evolution* **70**: 2909-2914.

Pollock, K., J. Hines, J. Nichols (1985). Goodness-of-Fit Tests for Open Capture-Recapture Models. *Biometrics* **41**: 399-410.

Pradel, R. (1993). Flexibility in Survival analysis from recapture data: Handling trap-dependence. Pages 29-37 in Lebreton & North, editors. *Marked individuals in the study of bird population*. Birkhäuser Verlag, Basel, Switzerland.

Pradel, R., Hines, J. E., Lebreton, J.-D. & Nichols, J. D. (1997). Capture-recapture survival models taking account of transients. *Biometrics* **53**: 60-72.

Pradel R., Wintrebert C.M.A. and Gimenez O. (2003). A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. *Biometrics* **59**: 43-53.

Pradel, R., Gimenez O. and J.-D. Lebreton (2005). Principles and interest of GOF tests for multistate capture-recapture models. *Animal Biodiversity and Conservation* **28**: 189-204.

Pradel R, Sanz-Aguilar A (2012) Modeling Trap-Awareness and Related Phenomena in Capture-Recapture Studies. *PLoS ONE* **7**: e32666.

R Development Core Team (2014) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Spendelov, J. A., D. Monticelli, J. D. Nichols, J. E. Hines, I. C. T. Nisbet, G. Cormons, H. Hays, J. J. Hatch, and C. S. Mostello (2016). Roseate Tern breeding dispersal and fidelity: responses to two newly restored

316 colony sites. *Ecosphere* **7**: e01510.

317 Supp, S. R., D. N. Koons, and S. K. M. Ernest (2015). Using life history trade-offs to understand core-  
318 transient structuring of a small mammal community. *Ecosphere* **6**: 187.

319 Warton, D. I., J. Stoklosa, G. Guillera-Aroita, D. I. MacKenzie and A. H. Welsh (2017). Graphical diagnostics  
320 for occupancy models with imperfect detection. *Methods in Ecology and Evolution* **8**: 408-419.

321 White, G. C. (2002). Discussant: The Use of Auxiliary Variables in Capture-Recapture Modeling: An  
322 Overview. *Journal of Applied Statistics* **29**: 103-106.